

EARLY MIOCENE SALAMANDERS AND LIZARDS FROM FLORIDA

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THE sediments of the Thomas Farm, Gilchrist County, Florida, enclose the remains of a diverse early Miocene vertebrate fauna, and since their discovery in 1931 have produced the only significant North American mid-Cenozoic record of vertebrate evolution east of the Mississippi River. A list of the vertebrate fauna and references may be found in Olsen (1962).

Some lower vertebrate fossils were recovered in early phases of collecting. These included *Alligator*, the turtles *Geochelone* and *Pseudemys*, and a few snakes. The snakes were described by Vanzolini (1952) along with a lizard jaw referred by him to a new species of *Peltosaurus*, *P. floridanus*. There is substantial doubt that this species is valid or that the fossil originally came from the Thomas Farm; this will be discussed below. Other snake material has been described by Auffenberg (1963).

The application of washing techniques for the recovery of microvertebrate remains has increased the representation of the fauna markedly. Among the lower vertebrates, the sirenid salamander *Siren hesterna* was described by Goin and Auffenberg (1955). Frogs are also abundant: *Rana*, *Bufo*, *Gastrophryne*, *Scaphiopus*, *Hyla*, and an extinct hylid *Proacris* have been recorded (see Holman, 1961, for references).

Additional material collected by the washing technique (see McKenna, 1962, for a discussion of this method) has been recently made available to me by the Museum of Comparative Zoology, Harvard University; Florida State Geological Survey; and the University of Florida. Additional records to the herpetological fauna are described below. The new material of frogs and snakes is being studied by J. Alan Holman.

ACKNOWLEDGMENTS AND ABBREVIATIONS

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konid anatomy. Ernest Williams read the manuscript critically. The National Science Foundation provided the necessary financial assistance through Grant G-18905, and the figures were prepared by Howard Hamman.

The following abbreviations are used: M.C.Z.—Museum of Comparative Zoology; U.F.—University of Florida; F.G.S.—Florida Geological Survey.

CLASS AMPHIBIA

ORDER URODELA

Family SALAMANDRIDAE

Notophthalmus robustus, n. sp.

Holotype: M.C.Z. no. 3384, dorsal vertebra.

Referred specimens: M.C.Z. nos. 3383, dorsal vertebra; 3385, first vertebra; nine other unnumbered specimens. U.F. nos. 6503, two dorsal vertebrae; 3597, dorsal vertebra; two unnumbered vertebrae. F.G.S., one unnumbered vertebra.

Diagnosis: A *Notophthalmus* differing from the Recent species in having more robust vertebrae, in which the neural spines are relatively low, and the rib-bearers relatively short and stubby.

Description: The type specimen and the other vertebrae are robust in general proportions. The maximum length of centrum in the type specimen is 2.0 mm. This is the largest of the vertebrae, though they are all approximately the same size. The centrum is opisthocoelous (pseudocoelous of Soler, 1950; see Estes, 1963, for a discussion of this subject), and the small, projecting condyle is set apart from the body of the centrum by a prominent constriction. The short, stubby rib-bearers are connected throughout their length by a sheet of bone, and the ventral rib-bearer connects anteriorly to the centrum by a well-developed or slight ventral lamina, depending on its position in the vertebral column. The zygapophyses are relatively small and are placed close to the centrum. The heavy neural arch is relatively low, and is capped by a flat-topped, sculptured, and pitted deposit of dermal bone that extends anteroposteriorly about two-thirds of the total length of the vertebra. On most of the vertebrae this ornament is badly broken, but in the type and a few others it is well preserved. In all but the

type it is of rather narrow side-to-side extent. The neural arch and dermal ornament are deeply notched posteriorly.

The first vertebra or "atlas" has a well-developed intercotylar process projecting anteriorly between the small oval cotyles, and the neural arch is expanded into a broad canopy over the neural canal anteriorly.

Discussion: Among Recent Salamandridae, only *Notophthalmus* and *Cynops* have neural spines capped by dermal bone having the same pattern as is seen here. *Cynops* is now restricted to Asia, and lacks the extensive pitting on the dermal cap of the neural spines found in *Notophthalmus* and the fossils. These fossils do not at all resemble the only other New World salamandrid, *Taricha*, from western North America, which lacks the dermal ornament on neural spines except on some anterior vertebrae. The fossil form differs from the several recent species of *Notophthalmus* (limited today to eastern North America) in having relatively more robust vertebrae, a condition that results in shorter, stubbier rib-bearers and a relatively lower neural spine. *N. robustus* is more different from the Recent species than they differ from each other, but the amount does not exceed interspecific variation in some other salamandrids. Most if not all of these differences can be traced to the more robust ossification in the fossil specimens. Fossil forms closely related to modern species often have more robust proportions than their descendants (see Goin and Auffenberg, 1955, for *Pseudobranchius*; Estes and Wassersug, 1963, for *Bufo*), and there is no particular reason why *Notophthalmus robustus* or related forms could not have given rise to the modern populations.

Family SIRENIDAE

Siren hesterna Goin and Auffenberg, 1955

Referred specimens: U.F. no. 6590, a broken dorsal vertebra.

Comments: This specimen differs from the material described by Goin and Auffenberg (1955) only in having a narrower angle (of about 100°) between the aliform processes. Their type specimen had a very wide angle (about 123°) between the aliform processes. Both specimens still greatly exceed the angular divergence between these processes known to occur in other fossil and Recent species of *Siren*.

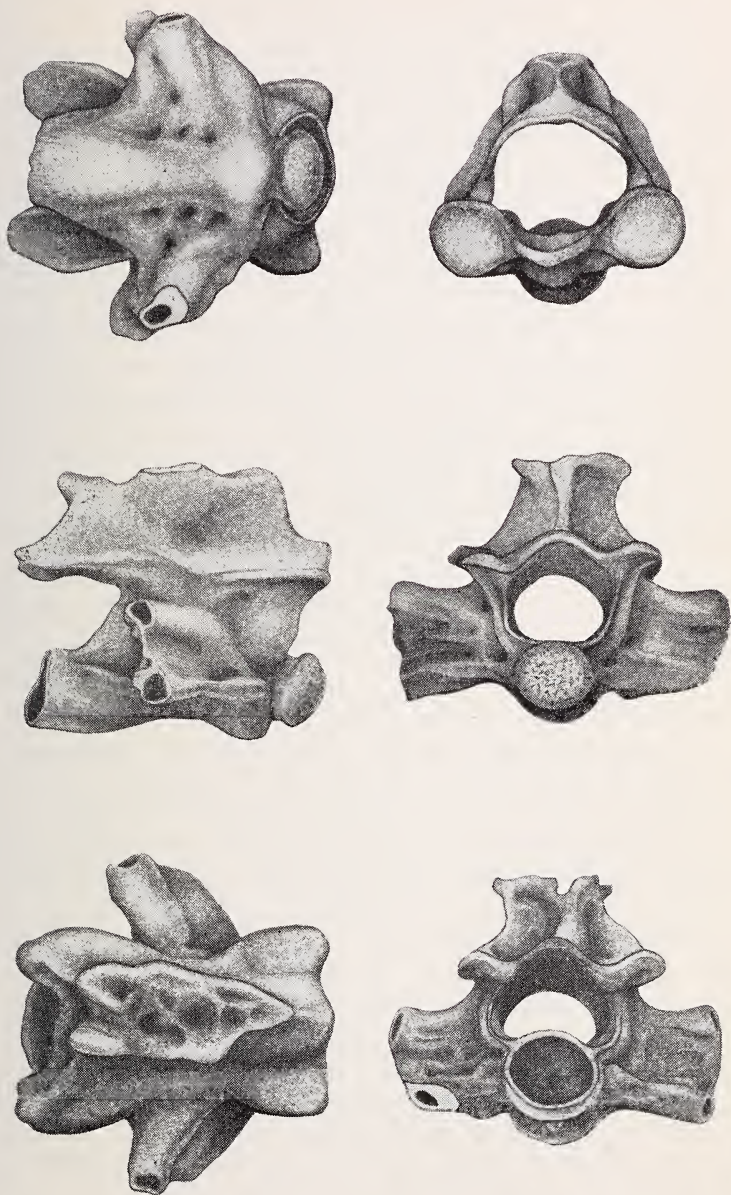


Fig. 1. *Notophthalmus robustus*, n. sp., ventral, right lateral, dorsal, anterior, and posterior views of dorsal vertebra, M.C.Z. no. 3384, type; upper right, anterior view of first vertebra, M.C.Z. no. 3385; all specimens X 20.

Family BATRACHOSAUROIDIDAE

Batrachosauroides dissimulans Taylor and Hesse, 1943

Referred specimen: U.F. no. 7802, a first vertebra ("atlas").

Description: The maximum width of the specimen across the cotyles is 14.3 mm, and maximum length of centrum at its mid-point is 7.5 mm. The tip of the neural spine is broken so that no height measurement is possible. The two deeply concave cotyles are suboval, and separated by a small, ridged intercotylar process which has only a small anterior projection. Several foramina are present on the concave ventral surface of the centrum. The neural arch is robust, and the posterior zygapophyses are well developed. The posterior cotyle is a deeply concave conical hollow. No ridges or laminae are present, and the bone is a solid, rounded, heavily ossified element.

Discussion: *Batrachosauroides dissimulans* is based on a large salamander skull from the Middle Miocene of the Texas Coastal Plain (Taylor and Hesse, 1943). Auffenberg (1958) described Lower and Middle Miocene vertebrae from the same region, referred them to *Batrachosauroides*, and established a new family for the genus. Auffenberg's reference of these vertebrae to *Batrachosauroides* is undoubtedly correct. The Thomas Farm specimen differs in no fundamental way from any of the six available similar elements from Texas. Auffenberg figured one of these Texas specimens (*ibid.*, fig. 1), but the figure is too diagrammatic to give any real idea of the contours of the specimen. The cotyles of this specimen are not as circular as he shows them, nor as regular on their surfaces. In reality, they approximate the suboval condition seen in the Florida specimen and duplicated in the rest of the Texas specimens.

The presence of *Batrachosauroides* in the Thomas Farm deposits is an interesting new record for this fauna. However, it is not surprising to find common herpetological taxa in the Texas and Florida localities, in view of the similarity of mammalian faunas, probable warm-humid environment, and latitude. Additional material of this interesting genus is now under study, and I hope to include a more comprehensive look at the relationships of this animal in a later paper.

CLASS REPTILIA

ORDER SAURIA

Family IGUANIDAE

Leiocephalus sp.

Referred specimens: M.C.Z. nos. 3378, fragment of right dentary; 3379, anterior tip of left dentary; 3380, fragment of jaw with two teeth. Nine jaw fragments, some with teeth, one fragment of right dentary showing association of teeth with edentulous dentaries of the type figured. Questionably referred are a number of dorsal and caudal vertebrae, a right scapulocoracoid, slightly broken, and a right innominate bone. U.F. no. 7803, fragmentary right dentary; six tooth-bearing fragments, and a premaxilla. Questionably referred are U.F. no. 5132, dorsal and caudal vertebrae and a distal end of a right humerus; U.F. no. 5745, four right and two left dentary fragments; and a premaxilla. F.G.S., four tooth-bearing fragments; two fragments of right, and two fragments of left dentaries; a badly broken right maxilla, which has the longest complete tooth row of any referred specimen. Questionably referred are two dorsal and two caudal vertebrae.

Description: The mandible is robust, and the Meckelian groove completely and smoothly fused for almost its entire length. The pleurodont teeth have tall, slim, and straight-sided shafts, except for a slight flaring toward the crown. The latter is flattened linguo-labially into a narrow tricuspid fan-shaped structure, the central cusp largest. Each side cusp is prominently separated from the main cusp by a wide groove, which fades out at the base of the crown. These grooves lack an associated ridge, seen in many such lizard teeth, which extends from the apex of the lateral cusp to the base of the crown. The anterior teeth are unicuspate, some with slight anterior and posterior crests, paralleling the formation of lateral cusps in the more posterior teeth. On the labial side of the dentary, a clearly marked but shallow trough near the posterior end of the tooth row marks the position of a coronoid overlap on the dentary.

Discussion: The admittedly fragmentary material associated here and referred to a Recent genus may appear a slim basis for such a conclusion. However, the association of the tooth fragments

with the edentulous jaws is based not only on the one specimen which shows these components in association, but for each specimen, on the characteristic pattern of pitting at the tooth bases, shape of tooth bases, spacing of teeth and similarity of preservation. In addition, the Museum of Comparative Zoology houses the best collection of iguanid skeletons available anywhere at the present time; it was prepared as a result of the generosity of the National Science Foundation. I have also been fortunate in having access to unpublished manuscripts by Richard Etheridge on *Leiocephalus* and *Anolis*, and by Dennis Staton on the construction of the iguanid mandible; I have profited a great deal by discussion of iguanid morphology and relationships with both of these gentlemen. Etheridge has suggested that the South American species of *Leiocephalus* are generically separate from the West Indian group. Among the many characters which he has used to separate the two groups is the consistent presence of flared, fan-shaped tooth crowns in the island forms; straight-sided columnar teeth in the South American species. This generic separation is followed here and indicated (until a new generic name is available for the South American species) by preceding each use of the generic name with the locality.

The fossil material can only be compared, on the basis of closure of the Meckelian groove and the form of the teeth, with observed species of the following living genera: *Brachylophus*, *Basiliscus*, *Plica*, West Indian *Leiocephalus*, *Liolaemus*, *Corythophanes*, and *Tropidurus*. Detailed tooth form, and presence of cusped anterior teeth eliminate *Brachylophus*. Complete fusion of Meckelian groove for much of the length of the dentary eliminates *Basiliscus*. The lack of a hyperpleurodont dentition (teeth reaching to or near the base of the dentary) excludes *Plica*. The lack of anteroposterior thickenings of the tooth shafts below the lateral cusps, and the relatively greater height of the teeth precludes comparison with *Tropidurus* and *Corythophanes*. Other forms not comparable with the fossil on the basis of non-flared tooth crowns are *Proctotretus*, *Stenocercus*, *Uranoscodon*, South American *Leiocephalus*, and *Urocentron*. *Hispaniolus pratensis*, which agrees closely with the fossils, is probably to be included in West Indian *Leiocephalus*, fide Etheridge. Thus, *Liolaemus* and West Indian *Leiocephalus* are the only genera which can be compared with the fossils on the basis of tooth shape and Meckelian groove closure, and most spe-

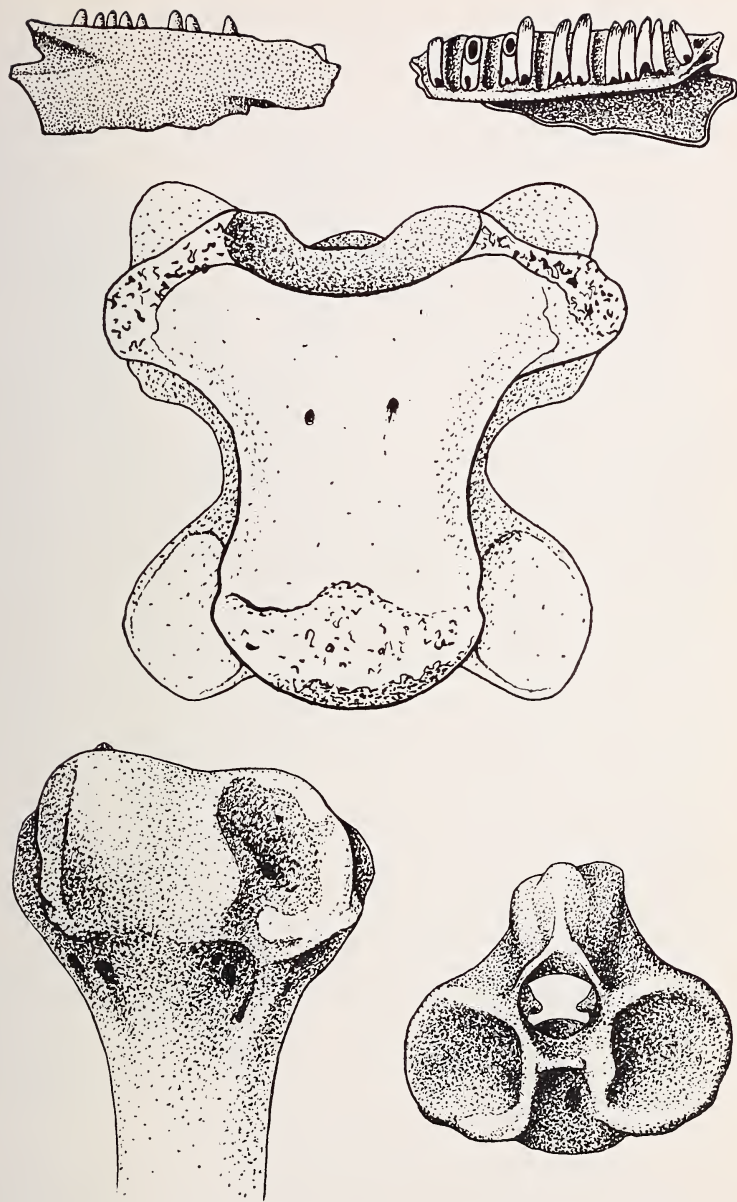


Fig. 2. Above, unidentified genus and species of Gekkonidae, labial and lingual views of right dentary fragment, M.C.Z. no. 3382, X 10. Center, unidentified genus and species of Anguidae, ventral view of dorsal vertebra, U.F. no. 1664; below left, the same, posterior view of distal end of right femur, U.F. no. 7806, both specimens X 6. Below right, *Batrachosauroides dissimulans*, anterior view of first vertebra, U.F. no. 7802, X 3.

cies of *Liolaemus* may be eliminated by the lack of flared tooth crowns.

Another character important in identification of the fossils is the presence of a posterodorsal shallow groove on the labial side of the dentary, shown in U.F. no. 7803 (fig. 3). This groove is covered in life by an anterior extension of the coronoid. Since this extension is present in *Liolaemus* and West Indian *Leiocephalus*, as well as a number of other iguanid genera, some discussion of the occurrence of this character is necessary.

The process is prominent, long, and slender in all of the "anoline" genera, and overlaps from one to as many as three of the posterior teeth. However, no "anoline" possesses fan-shaped teeth, and this group is excluded from further consideration here. Many of the so-called "iguanine" genera also possess this process; among these, *Dipsosaurus*, *Amblyrhynchus*, *Conolophus*, *Sauromalus*, *Brachylophus*, *Cyclura*, and *Iguana* all have a broad, wedge-shaped coronoid extension, rather than the long, dagger-like one seen in the fossils. In addition, all of these genera have quite different tooth shapes, much increased cuspsation, short deep jaws, or a combination of these which serve to distinguish them from the fossils. Juvenile *Ctenosaura* have teeth very similar to those of the fossils, and also show an overlap of as many as three teeth of the posterior dentary row by the coronoid extension, as in the fossil. However, this much overlap occurs only in the largest specimens of *Ctenosaura*, many times larger than the fossils. No overlap of teeth by the process is present in juveniles of size comparable with the fossils, and in any case, the coronoid extension in *Ctenosaura* is primarily of the broad, wedge-shaped type mentioned above.

Enyalioides, *Morunasaurus*, and *Hoplocercus*, "iguanines" which have a dagger-shaped coronoid extension, all differ from the fossil in having open Meckelian grooves (broadly open, with large splenial, in the latter two). In tooth form, *Enyalioides* has a more fan-shaped crown with a tendency to multiply cusps beyond three, while the latter two lack fan-shaped teeth entirely.

Among the remaining iguanids, grouped essentially as "tropidurine" and "sceloporine" types, only West Indian *Leiocephalus* and *Liolaemus* possess a coronoid extension of any type. In these two genera, this process extends a variable distance anteriorly. In fifteen available species of *Liolaemus* it usually overlaps two teeth at the posterior end of the row, but may either overlap three or

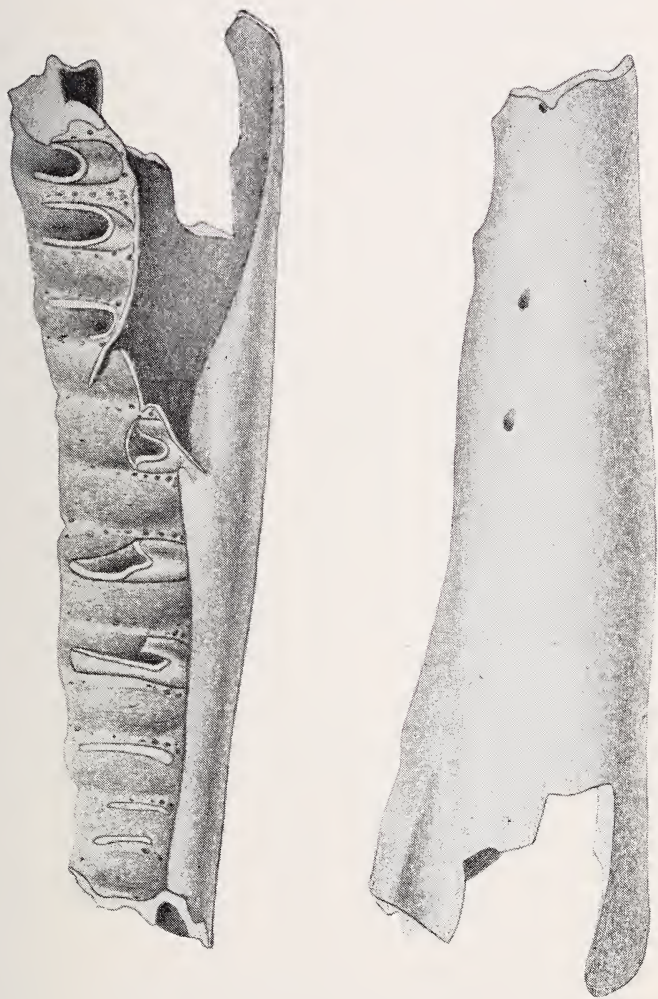


Fig. 3. *Leiocephalus* sp., lingual and labial views of right dentary, U.F. no. 7803, X 10.

none at all. In West Indian *Leiocephalus* it may be much better developed, and in *L. c. carinatus* may overlap the last five dentary teeth, though again two is the most frequent condition. A small amount of breakage obscures the true outline of the posterior end of the tooth row in U.F. no. 7803, but it is clear that at least three and perhaps four teeth were overlapped by the coronoid extension. If the latter is the case, it is another condition suggestive of West Indian *Leiocephalus*, but unfortunately this cannot be determined at this time.

However, several other considerations make West Indian *Leiocephalus* a more probable choice than *Liolaemus*. First, only one species of *Liolaemus*, *L. platei*, has teeth showing as pronounced a crown flare as in all West Indian *Leiocephalus*. *Liolaemus annectens*, *L. multiformis*, and *L. nigromaculatus* have weakly flared teeth, less so than in the fossil specimens and West Indian *Leiocephalus*. The other species lack flared teeth. Second, *Liolaemus* tends to have a relatively short dentary when compared with West Indian *Leiocephalus* and the fossils. Though the fossil dentaries are all broken anteriorly, their length and slenderness are still immediately apparent. Third, the Meckelian groove is open in eight of the species of *Liolaemus* available to me, and while the other seven show a fused condition, in no case is this as complete or as antero-posteriorly extensive as in West Indian *Leiocephalus* and the fossils.

On zoogeographic grounds the choice of West Indian *Leiocephalus* or *Liolaemus* becomes a West Indian vs. a South American one. Although little if anything links Florida faunistically to the West Indies during the Miocene, or for that matter at any other time, I believe that the close proximity of Florida to the Antilles makes it as likely a linkage in this case as one to South America, which was also separated from North America at this time and for some time previously.

In summary, a number of individually rather inconclusive morphological characteristics combine to strengthen confidence, I believe, in the premise that West Indian *Leiocephalus* is the most probable group to which the fossils may be referred. Since the type species of *Leiocephalus* is *L. carinatus* from Cuba, the generic name will remain with the island forms and with these fossils.

Unidentified IGUANIDAE

A number of specimens, described below, indicate that other iguanids are present in the Thomas Farm fauna. These are here referred to three unnamed species A, B, and C. By analogy with Recent iguanids, the differences between these three species suggest (insofar as the scanty material permits) that they belonged to three different genera, none of which can be identified at the present time.

Unidentified genus, species A

Referred specimens: M.C.Z. no. 2590, two teeth in a small fragment of maxilla; a single unnumbered tooth.

Description: The specimen has relatively short-crowned teeth, with rather plump bases. The main cusp is quite large and projects strongly from the occlusal surface of the tooth, and is flanked by relatively weak side cusps. The single tooth is similar, but has a more swollen base and relatively smaller main cusp.

Discussion: The label in the box in which M.C.Z. no. 2590 was found identifies the specimen as *Anolis* (?) sp., and it does resemble some of the anoles, as well as some other iguanids, in details of tooth shape; especially the combination of rather plump-based teeth with a strongly projecting main cusp. If the two specimens come from individuals of the same species, they represent different areas in the tooth row, the single tooth probably being from near the posterior part of the series. The specimens are clearly distinct from the West Indian *Leiocephalus* specimens described above, but do not warrant more precise identification.

Unidentified genus, species B

Referred specimen: U.F. no. 7804, a single fragment of left dentary.

Comments: The specimen represents an iguanid with an open Meckelian groove, and is thus distinct from the West Indian *Leiocephalus* described above. Minor differences in attachment and spacing of teeth and in the pattern of pitting at the bases of the teeth also distinguish the specimen. If the teeth described above as species A could be shown to belong to the anoles (all of which have closed and fused Meckelian grooves) then this jaw would represent a third iguanid in the Thomas Farm fauna. On the

other hand, the only evidence which indicates at this time that A and B might belong together is that of parsimony. There appears to have been a difference between A and B in crown height of teeth, but as this is inconclusive they are separated here principally to indicate the potential diversity of the iguanids in this fauna.

Unidentified genus, species C

Referred specimens: U.F. no. 7805, anterior end of left dentary; an unnumbered sacral vertebra.

Description: The fossil dentary is from an individual several times larger than those representing the fossils referred to West Indian *Leiocephalus*. The Meckelian groove is closed and fused. The tooth crowns are broken and worn away, and their bases are relatively closely spaced. The area where the teeth attach to the jaw is smooth, and lacks the regular pattern of tiny foramina seen in West Indian *Leiocephalus*. The tooth shafts are deeper at their bases than in West Indian *Leiocephalus*, and their lingual faces are straight, rather than having the slight concavity seen in the latter. The vertebra is of iguanid type, and has a strong zygosphene-zygantrum articulation.

Discussion: The thickness of the teeth at their bases resembles the condition seen in iguanids having broadly leaf-shaped multi-cusped teeth (e.g. *Iguana*, *Cyclura*, etc.). The best character separating this form from West Indian *Leiocephalus* is the difference in pattern of tiny foramina at the tooth attachment area. The greater size probably also differentiates this form from the latter, but in the absence of other more clear-cut characteristics, is of doubtful validity. The vertebrae referred to West Indian *Leiocephalus* also have zygosphenes and zygantra; thus size alone allows reference of the large vertebra to species C.

Summary of Thomas Farm Iguanidae

The presence of West Indian *Leiocephalus* or of a very closely related form is well documented. Fragmentary specimens allow the speculation that as many as three other iguanid species (probably belonging to three different genera) were present: species A, based on teeth having resemblances to some of the anoles; species B, based on a dentary having an open Meckelian groove; and species C, a large form perhaps related to one of the large *Iguana*-

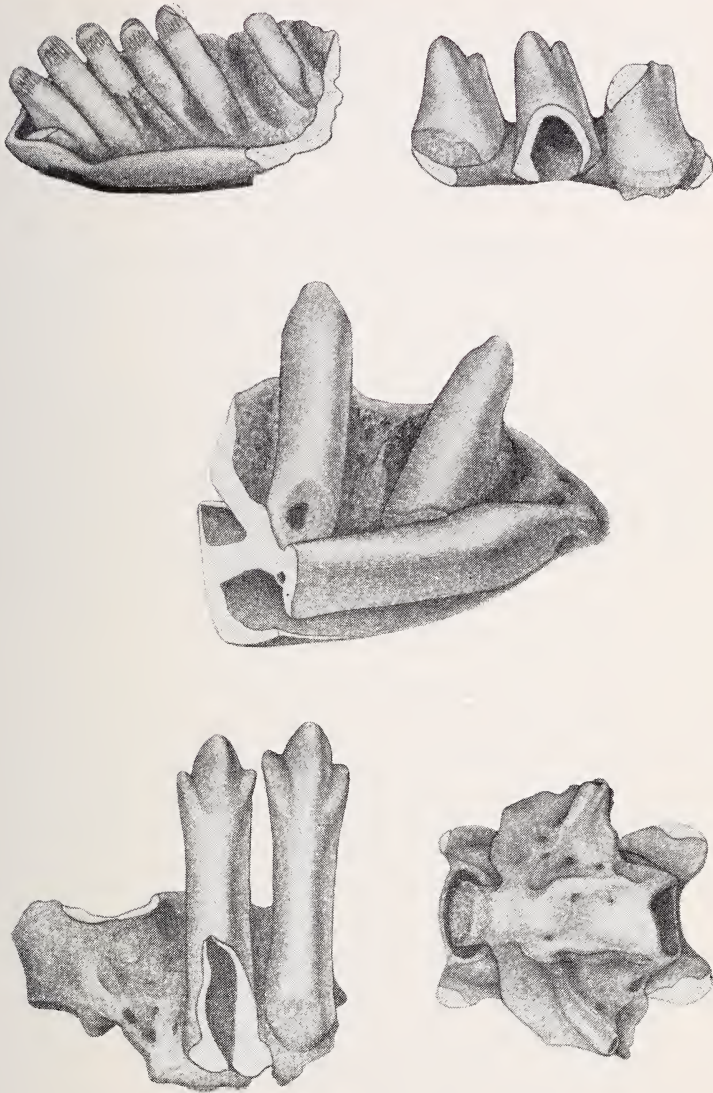


Fig. 4. Above left, *Eumeces*, sp., lingual view of anterior end of right dentary, M.C.Z. no. 3377. Above right, *Cnemidophorus* sp., lingual view of tooth-bearing fragment, probably from posterior part of maxillary or dentary series, M.C.Z. no. 3381. Center, *Leiocephalus* sp., lingual view of anterior tip of left dentary, M.C.Z. no. 3379; below left, the same, lingual view of jaw fragment bearing two teeth, M.C.Z. no. 3380. Below right, *Notophthalmus* sp., ventral view of dorsal vertebra, M.C.Z. no. 3383. All specimens X 20.

like genera. The physical possibility exists that species A and B may be synonymous, since one is based on teeth, the other on a dentary. Yet no evidence exists at this time for either alternative. I believe that species C is distinct, but without knowledge of the tooth crown pattern a firm decision cannot be made.

Family GEKKONIDAE

Unidentified genus and species

Referred specimen: M.C.Z. no. 3382, posterior tooth-bearing fragment of right dentary.

Description: The fragment bears spaces for sixteen teeth, of which eight are complete. These teeth are simple, pointed cones, lightly striated at their tips. They are rather irregularly spaced and variable in height and individual contour. At the posterior end of the tooth row there is a tiny facet for a lingual process of the coronoid. Just medial to the tooth row, the dentary is broken, with loss of the medial edge of the *sulcus dentalis*. Labially the bone is smooth, and the remains of a foramen are present antero-ventrally. Posterodorsally there is a deeply-incised notch for the labial extension of the coronoid.

Discussion: The combination of numerous, small, slightly irregular, conical teeth and the deeply-incised notch for a labial extension of the coronoid is characteristic of most of the geckos. This fossil is nearly identical with Recent and fossil individuals of many different genera. The striations are variable and infrequently occurring in most modern forms, but when they do occur they are found only on the posterior teeth. I believe that there is little doubt that this fossil represents a gecko, but the lack of distinguishing characteristics in dentaries of most Recent forms precludes more specific identification.

Family SCINCIDAE

Eumeces sp.

Referred specimens: M.C.Z. no. 3377, anterior end of right dentary; two other unnumbered fragments of left dentary, one unnumbered fragment of right dentary, and two tooth-bearing fragments.

Description: The dentary fragments all show an open Meckelian groove and a slight *sulcus dentalis*. The teeth are columnar; closely and regularly spaced. The crowns are blunt, and their external surface is smooth, lingually curved, and bluntly obtuse. Most of the crowns show some evidence of wear on the tips. The inner surface of the crowns is concave and coarsely striated. The striations are short and come to an abrupt end at the base of the crown.

Discussion: The crown pattern of obtuse smooth labial side and prominently striated lingual surface, in combination with the regular and close spacing of the teeth, is unique to some species of *Eumeces*. Within the group there seem to be no strong geographical patterns as far as the various types of tooth crown patterns are concerned; these specimens resemble species from California, the Ryukyu Islands, and Kansas as much as they do the ones living in Florida today. *Eumeces* has already been recorded from the late Pliocene of North America (Taylor, 1941) and this fossil extends the record of this diverse and widely spread genus back to the early Miocene.

Family TEIIDAE

Cnemidophorus sp.

Referred specimens: M.C.Z. no. 3381, tooth-bearing fragment, probably from the posterior part of maxillary or dentary series. U.F., unnumbered fragment of right maxilla; unnumbered anterior end of right dentary. F.G.S., two tooth-bearing fragments; two fragments of right dentary; some doubtfully referred caudal vertebrae.

Description: The teeth are short near the rear of the jaw, as indicated by the figured specimen, but increase in height toward the front as indicated by the other specimens. The tooth bases are slightly swollen, and the shafts taper to the crown. The latter is bicuspid on all specimens, with the anterior cusp the smaller. Implantation is subpleurodont. The wide shelf under the tooth-bearing process indicates that the figured teeth come from the posterior part of the dentary or maxillary series. A referred dentary from the University of Florida collection is slender, pinched or narrowed near its anterior end, and has a narrowly open Meckelian groove.

Discussion: The so-called microteiids may have either bicuspid or tricuspid teeth in the posterior series, but none of them have the slender, narrowed dentary seen in the fossils, nor do any of the other lizards which possess bicuspid teeth. Among the more primitive teiids, only *Ameiva* and *Cnemidophorus* have bicuspid teeth of this sort in the posterior series associated with the slender dentary. *Callopiastes* has similar teeth, but they differ in having the main cusp very much larger than the tiny anterior cusp, and the jaw shape is quite different. The other genera either have tricuspid posterior teeth or a dentition otherwise modified toward a crushing type. *Ameiva* and *Cnemidophorus* (through the taxonomy of the species usually referred to the latter is hopelessly snarled) show little to differentiate them as full genera. It has been stated (Burt, 1931) that the "retractile" tongue distinguishes *Ameiva*, but I am not certain that this is consistent or of sufficient importance for generic separation. Certainly they are very closely related, as closely as *Diploglossus* and the now synonymous *Celestus*, which were long separated on a character of no greater significance.

A practically complete representation of species of *Ameiva* and *Cnemidophorus* has been examined with respect to the presence of tricuspid or bicuspid teeth and associated characters. Among the species now grouped as *Ameiva*, bicuspid teeth occur only in the West Indian species (most consistently in the Lesser Antillean forms), though some island species, e.g. *A. exsul*, have tricuspid teeth in the posterior part of the series. No South or Central American *Ameiva* was found to have bicuspid teeth. Teeth of *Cnemidophorus* may be bicuspid or tricuspid posteriorly; some species seem to have consistently one condition or the other, in others there is considerable intraspecific variation. In addition, there seems to be no consistent geographic grouping; the two conditions appear indiscriminantly in South, Central, or North American populations. Identification of these fossils with *Cnemidophorus* rather than with *Ameiva* is primarily on the basis of zoogeographic probability. Since the primary affinity of the Thomas Farm fauna is with North America, it is perhaps more probable that the affinities of the fossils would lie with forms that are known to have been in North America as far back as the early Pliocene (Taylor, 1941 and an unpublished record from the Valentine formation in Nebraska) and that seem to have their affinities with the modern North American *Cnemidophorus*. However, the presence of West Indian *Leio-*

cephalus in the Thomas Farm fauna demonstrates that we cannot be sure that these fossils are not related to the bicuspid island ameivas.

Family ANGUIDAE

Unidentified genus and species

Referred specimens: U.F. no. 1664, complete dorsal vertebra; U.F. no. 7806, complete right femur; three other unnumbered vertebral fragments and the distal half of a left femur.

Description: The dorsal vertebra is robust, has a relatively low neural arch, small neural canal, broad zygapophyses, and lacks zygosphenes or zygantra. The centrum has concave sides when viewed ventrally, and two tiny subcentral foramina are present. The condyle is slightly abraded, but there is a slight constriction between the centrum and the wide, flattened condyle itself. One of the unnumbered vertebrae is one-half of a caudal, lacking zygosphenes, and showing clearly the presence of caudal autotomy. The other vertebrae are broken but conform to the figured specimen.

The femur has a wide, flared head, which is well separated from the trochanter major. The shaft is relatively short, and the distal articular end strongly flared. There is a well-developed popliteal fossa. The ligamentary pit between the tibial attachment surfaces is deep and irregularly shaped.

Discussion: The general shape of the vertebrae, with the low neural arch, small neural canal, and slight constriction between condyle and centrum (not to be confused with the precondylar constriction of varanoids) are characteristically anguid. The breadth of the condyle and the strongly concave ventral sides of the centrum distinguish these vertebrae clearly from those of *Peltosaurus*, in which the condyle is quite narrow and the sides of the centrum relatively straight, as in *Gerrhonotus*. In these two characters and in general aspect the fossils resemble the vertebrae of *Heloderma* (and to a slight degree those of *Ophisaurus* as well, though the ventral surface of the centrum is not flattened as in that genus, and the femora, if correctly referred, indicate a limbed form). Hoffstetter (1957, fig. 6) figures a similar vertebra for *Eurheloderma gallicum*, but it is less extreme than this specimen in centrum shape. The caudal vertebra indicates an autotomous condition of the tail, an anguroid rather than a varanoid character-

istic. This caudal was referred on the basis of size, general form, and lack of zygosphenes. The only other large lizard known in the Thomas Farm fauna is a large iguanid (discussed above as unidentified genus, species C) which has strong zygosphene-zygantrum articulations on all referred vertebrae.

The femur also resembles that of *Heloderma* in the widely flared head and distal condyle. The short, stubby shaft of the bone indicates an animal with relatively short legs; a condition common in larger anguroids. The ligamentary pit between the tibial articulations may eventually prove to be useful in separating genera of anguids, when enough material has accumulated so that the pattern of variation can be understood. At this time, all that can be said is that the pattern differs from the condition seen in large *Diploglossus* and fossil *Glyptosaurus*. Recent *Gerrhonotus* is too small to make any meaningful comparison, as are the other Recent anguids, and the femur of *Peltosaurus* is unknown.

In summary, these fossils, if they belong together, seem to indicate a large, limbed anguid showing some similarities to *Heloderma*. The shape of the vertebrae are quite distinct from those of *Peltosaurus*, and in any case, the record of *P. floridanus* Vanzolini is open to question, as discussed below.

A NOTE ON THE STATUS OF *Peltosaurus floridanus*

Vanzolini (1952, p. 457), in describing the type specimen of *Peltosaurus floridanus* (M.C.Z. no. 1799), stated that the lateral dentary process of the coronoid reached farther forward than it did in *Glyptosaurus* or in other species of *Peltosaurus*. In species of both of these two genera, the lateral dentary process of the coronoid reaches to about the level of the last dentary tooth, and this is also true of M.C.Z. no. 1799.

The color of the bone of M.C.Z. no. 1799 is a pale and uniform cream, and a fine-grained, greyish-white matrix adheres in places. Stanley J. Olsen has confirmed that this matrix is unlike that of the Thomas Farm deposits, and that the natural unweathered color of Thomas Farm fossils is dark brown; M.C.Z. no. 1799 is not at all weathered. On the other hand, preservation and matrix closely resemble specimens from the Oligocene White River Formation, in which *Peltosaurus granulosus* is found. It seems probable that this specimen was actually from the White River Formation and

was mistakenly placed in the box containing the specimens described by Vanzolini before he received them.

In view of this, and the absence of the distinguishing characteristic cited by Vanzolini, *Peltosaurus floridanus* is here placed in the synonymy of *P. granulatus* Cope. It is possible that the latter or a related form might occur in the Thomas Farm fauna (though I consider it improbable, and the large anguid noted above seems clearly unrelated to *Peltosaurus*), but at the present it seems best to remove the record from the faunal list.

ENVIRONMENT OF THE THOMAS FARM

The most generally accepted interpretation of the Thomas Farm deposits is that they represent the filling of a sinkhole in a porous, eroded, limestone terrain. Lack of fish remains appears to preclude connection with major stream systems, though it does not preclude small streams and ponds as part of the internal drainage pattern of the sinkhole. The presence of *Siren*, an aquatic salamander, has been thought to imply a relatively permanent source of water, but there are so few specimens that it is possible to explain the occurrence of this animal as an introduction by a predator (though I consider this unlikely). However, the abundant frogs, *Pseudemys*, and alligators indicate a pond or pool environment, so that it is fairly clear that some source of relatively permanent water was available.

Sirens live today in primarily quiet, stagnant waters, and are often found associated with vegetation mats in these localities. Recent *Notophthalmus* has such broad geographic spread and ecologic tolerances that no statements about the fossil form are warranted. Though both larvae and mature adults of this genus are aquatic, there is often a terrestrial eft stage, and at this time it is not possible to distinguish late larvae, efts, and adults on the basis of vertebral characters. The habits of *Batrachosauroides* are unknown. The absence of extensive bony crests, ridges, and keels on vertebrae of this form probably indicates that there was no extensive diversification of muscle masses usually associated with an attenuated body form, reduced limbs, and aquatic habit. However, the skull (Taylor and Hesse, 1943) indicates at least a partially larval or neotenic form, and modern analogues are invariably aquatic.

The lizards described here have (with one exception) wide ecologic tolerances and widespread geographic occurrence (*Eumeces*, *Cnemidophorus*), or are too poorly known for comment (all others except West Indian *Leiocephalus*). Island species of *Leiocephalus* occur today mainly in open country, and though most of the species are found in dry locations, some may also occur in damp areas.

Some of the fossil mammals (e.g. kangaroo rat, badger), insofar as these more rapidly evolving forms can be used for ecologic interpretation, also indicate relatively dry, open country, while others (e.g. the browsing horses) indicate forested situations. Thus the spectrum of habitat types found in this one deposit is broad, ranging from the relatively clear-cut aquatic habit of *Siren* and the pondside frogs, through forest dwellers, to inhabitants of dry open areas. This situation is most plausibly interpreted as a sink-hole with internal drainage (probably spring-fed, since connection with other drainage systems would be indicated by the presence of fresh-water fishes) which, as a result of the available water, drew to it animals from diverse habitats. To attract large numbers of both browsing horses and other animals adapted for dry, open country, it was probably in an ecotone between the two habitats. Perhaps there were dense thickets, or forested areas capping limestone bluffs, at the foot of which, under the massive overhanging limestone blocks, were found pools suitable for water holes. These pools supported aquatic and pondside vertebrates and might have been on the margins of more open dry country, thus attracting many plains types. The adjacent forested area would provide access for the browsers, and overhanging limestone cliffs would provide suitable habitat for the many bats also represented in the deposit. Auffenberg (1963) has interpreted the deposit as a linear fissure in the underlying limestone, in which the vertebrate remains were deposited. This fissure, which was certainly a large one, was probably part of a depression in locally-developed karst topography, as Auffenberg has suggested. The disarticulated nature of all of the Thomas Farm fossils would imply that the bones remaining after maceration were subsequently washed into the fissure, rather than the latter being a primary trap for the animals.

AFFINITIES OF THE FAUNA

Of the eleven herpetological taxa identified in this paper, it is possible to apply generic names to only six. Of these six, four (*Siren*, *Notophthalmus*, *Eumeces*, *Cnemidophorus*), occur in Florida today, one (*Leiocephalus*) is of West Indies affinities, and one (*Batrachosauroides*) is extinct but associated in the fossil record with other warm-humid faunas.

Similarity to the Recent Floridan fauna is heightened when the other reptiles (*Alligator*, *Pseudemys*, *Geochelone*) and amphibians (*Bufo*, *Rana*, *Gastrophryne*, *Hyla*, *Scaphiopus*) are considered. The extinct *Proacris* is the only frog not occurring there today. Thus at least twelve Recent herpetological genera have been in Florida since the early Miocene.

It is to be expected that other modern elements will be found as more material becomes available. If the large anguid vertebrae described above could be shown to pertain to *Heloderma* (as their morphology suggests) this would be an interesting intermediate record of helodermatids more closely linking the Eocene-Oligocene *Eurheloderma* of France and *Heloderma matthewi* from the Oligocene of Nebraska to the Recent distribution of this genus.

The presence of a modern West Indian type of *Leiocephalus* in the Florida Miocene is one of the few resemblances of the terrestrial vertebrate faunas between the two areas. It must not be taken, however, as evidence for land connection of any sort. At present, without greater knowledge of fossil distributional patterns and lacking greater faunal similarity between the two areas, it must be interpreted as a sweepstakes occurrence.

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